Correcting for allometry in studies of fluctuating asymmetry and quality within samples

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Fluctuating asymmetry (FA) refers to deviations from perfect symmetry in a bilateral character and is believed to reflect an organism's quality. However, allometric relations between asymmetry and trait size may confound FA–quality relations. Larger traits may have more ‘opportunity’ to become asymmetric. Thus, researchers suggest that if allometric relations between FA and size are found, some correction for size is needed (typically FA scaled by size). I used a simulation model to examine potential consequences of allometry for detection of FA–quality relations within samples and examined efficacy of rules currently used to correct for size. Consequences of allometry can be severe, causing up to 77% type I errors or 98% power loss when true FA–quality relations exist (when FA–size relations are isometric), depending upon the strength and direction of size–quality relations. I illustrate why current rules to correct for size are inefficient and suggest alternative rules. Problems of allometry that require further attention are discussed.

Keywords: allometry; fluctuating asymmetry; quality; simulation model

1. INTRODUCTION

Fluctuating asymmetry (FA) refers to small directionally random deviations from perfect bilateral symmetry ($FA = |\text{right} - \text{left}|$) and is believed to reflect an organism's developmental stability (DS; i.e. ability to buffer or resist disruption of precise development (Palmer 1994)). Individuals of higher quality putatively have higher DS and lower FA on average. Thus, FA may reflect quality of individuals (Polak & Trivers 1993). Surrogate measures of quality typically related to FA include life-history traits such as survival or number of offspring (reviewed in Leung & Forbes (1996)). Cumulative results suggest that FA–quality relations exist as predicted, but are weak on average and heterogeneous (Leung & Forbes 1996).

FA relations may be weak and heterogeneous because allometric relations (i.e. FA–size) confound FA–quality relations. Traits that grow larger may have more ‘opportunity’ to become asymmetric, resulting in positive FA–size relations; e.g. FA of legs may be greater than ears because legs are larger than ears rather than because DS differs. Relative FA (FA scaled by trait size; $FA_{\text{rel}} = 0.5 \times |\text{right} - \text{left}| / (\text{right} + \text{left})$) is the method most commonly suggested and used to correct for allometry (Palmer 1994), although a few studies have used other methods (for example, multiple regression (e.g. Solberg & Sether 1993) and partial regression (e.g. Harvey & Walsh 1993)). However, FA may not relate to size in all traits, and corrections should be done only when there is clear evidence for FA–size relations (Palmer 1994). Typically,

allometric relations are detected using significance of FA–size correlations as a criterion.

Swaddle *et al.* (1994) noted that FA_{rel} is valid only when FA–size relations are isometric (i.e. FA is proportional to size). However, isometry rarely has been tested (but see Møller 1992; McLachlan & Cant 1995). Further, researchers have not examined explicitly the consequences of using FA_{rel} when FA–size relations are anisometric (i.e. not isometric); neither have they examined efficacy of tests for isometry, nor suggested alternative methods. In addition, researchers have suggested that size corrections may obscure FA–quality relations if size relates to quality (Palmer 1994); again, no study has explicitly examined the consequences of size–quality relations.

In this paper, I used a simulation model to determine potential consequences of allometry and to suggest rules to correct for size (hereafter simply termed rules). I used type I error rates (finding significant FA–quality relations when no underlying relations exist) and power (probability of finding significance when true FA–quality relations exist) as criteria to judge the efficacy of different rules. Mathematical models allow the presence or absence of FA–quality, FA–size and size–quality relations to be specified. Thus, we can examine conditions where inflated type I error rates occur and compare the power of different rules. In empirical studies, different rules may yield different results; however, we would not know whether differences occurred because of increased type I error rates or increased power.

2. BASIC MODEL

FA_u and FA_{rel} refer to absolute FA uncorrected for size and absolute FA divided by average trait size, respectively. Equations simulated three relations: (i) component of size variation related to quality variation, (ii) component of FA_u variation related to size variation, and (iii) component of FA_u variation related to quality variation (quality represented any measure that researchers could relate to trait size or FA; e.g. survival). FA_u was defined as

$$FA_{ui} = |R_i - L_i| \quad (1)$$

where R and L were the right and left trait sizes of individual i , respectively. Trait sizes were determined by summing growth magnitudes (g) and asymmetry in growth (A) across j growth intervals for individual i . I assumed that A was directionally random; thus R could be less than or greater than L and $(R-L)$ would be distributed around a mean of zero. In notation,

$$R_i = \sum (g_{ij} + A_{ij}), \quad (2)$$

$$L_i = \sum g_{ij}. \quad (3)$$

Growth (g) was modelled as

$$g_{ij} = \mu + \alpha \times f(q_i) + \beta \times V_i, \quad (4)$$

where μ was mean growth, $f(q)$ was a function of quality, and V was variation in growth independent of quality. α and β were constants describing relative contributions of q and V to growth (e.g. if $\alpha:\beta$ was 1:0 and 0:1, quality would account for 100% and 0% of size variation, respectively). $f(q)$ and V followed normal distributions (mean, $\bar{x}=0$; standard deviation, $\sigma=1/3$). μ was set at 10. I considered both positive ($\alpha>0$) and inverse ($\alpha<0$) size–quality relations. I allowed two growth intervals (j). I did not consider perfect size–quality correlations ($\alpha:\beta=0:1$; unlikely in nature although size–quality relations can be strong).

Developmental noise (DN) increased A and was modelled as

$$DN_{ij} = a \times f(g_{ij}) + b \times c, \quad (5)$$

where $f(g_{ij})$ was a function of size, a and b were constants determining contribution of size on asymmetry, c denoted processes independent of size but which affected DN, and subscripts were as above. $f(g_{ij})$ and c followed normal distributions ($\bar{x}=0$; $\sigma=g_{ij}/300$ and $1/300$, respectively). Standard deviations were small such that FA comprised only a small proportion of trait size (Swaddle *et al.* 1994). As the ratio $a:b$ increased, the contribution of size on A ($f(g_{ij})$) increased relative to other processes (c) (e.g. if $g_{ij}=10$ for all individuals, and $a:b=0.1:1$, relative contribution of size on A would be 1:1 because $f(g_{ij})$ was scaled by size). When $a:b$ was 1:0, DN was isometrically related to size. I also examined anisometric relations where DN_{ij} was proportional to growth squared ($f(g_{ij}^2)$) has $\bar{x}=0$ and $\sigma=g_{ij}^2/300$).

Developmental stability (DS) reduced the effect of DN on A :

$$A_{ij} = DN_{ij}/(1 + DS_i) \quad (6)$$

and

$$DS_i = \delta \times q_i, \quad (7)$$

where δ was a constant determining the magnitude of DS. I modelled DS as a linear function of quality (q), where q explained all the variation in DS. Although other variation exists in nature, such variation only weakens relations between A and q and was not important for this model. Different strengths of A – q relations were generated by varying δ (the strength of A – q relations increased as δ increased).

The purpose of this model was to examine the validity of rules, to determine the potential consequences of allometry and to compare the efficiency of different rules. I examined the validity of rules using type I error rates (i.e. when $\delta=0$). If error rates were reasonably low (compared with the predicted alpha of 5%), I examined power (i.e. when $\delta>0$). I determined consequences of allometry using relative power (RP); i.e. power of rules in the presence of allometric relations relative to power of FA_u in the absence of FA–size relations. FA_u in the absence of FA–size relations represented results that we should expect if allometry was not a confounding factor, and was a baseline for comparison. I examined the efficiency of rules for size correction under given allometric relations, using differences in absolute power (DP) between rules and FA_u under those given allometric relations. Thus,

$$RP = [(\text{power of rule in the presence of allometric relations}) / (\text{power of } FA_u \text{ in the absence of allometric relations})] \times 100\%, \quad (8)$$

$$DP = \text{power of rule} - \text{power of } FA_u \quad (\text{both in the presence of the same allometric relations}). \quad (9)$$

I ran 1000 simulations for each of 200 sets of parameter values (sample sizes $N=40$ and 100, five size–quality relations ($\alpha:\beta$), five FA–size relations ($a:b$) and four FA–quality relations (δ); see Appendix A for values. Electronic appendices A and B can be found at http://www.pubs.royalsoc.ac.uk/publish/pro_bs/sep98pb1.htm). I primarily considered FA–size relations ranging from no relation ($a:b=0:1$) to isometric ($a:b=1:0$). However, I ran additional simulations for FA–size relations greater than isometry ($FA \propto \text{size}^2$) using only parameters that produced the greatest consequences of allometry (see below).

I examined 11 rules based on FA_u , FA_{rel} and multiple regressions (MR) and different criteria to determine when size corrections should be conducted (table 1). Rules included conducting size corrections when FA–size relations were significant or correcting using FA_{rel} only when FA–size relations were isometric (Swaddle *et al.* 1994). I identified departures from isometry following Niklas (1994). Statistics generated by simulations were compared with Statistica and SAS, to ensure accuracy of the model. All tests were based on one-tailed hypotheses predicting inverse FA–quality relations.

3. POSITIVE SIZE–QUALITY RELATIONS: CURRENT RULES

I considered rules 1 to 7 to be the current rules for size correction (table 1). In the absence of size–quality

Table 1. *Description of rules used in this paper*

(Suggested rules are indicated by an *.)

rule	description
1	Use FA_u regardless of the strength of FA–size relations.
2	Use FA_{rel} regardless of the strength of FA–size relations.
3	Use FA_{rel} only when FA–size relations are significant; otherwise use FA_u . This is the most common rule currently used. *Use rule 3 if the coefficient of variation of size (CV) is small.
4	Use FA_{rel} only when FA–size relations are isometric; otherwise use FA_u . Deviation from isometry was identified by an intercept significantly different from zero in the regression between $ FA $ and size (Niklas 1994).
5	Use FA_{rel} only when FA–size relations are isometric; otherwise use FA_u . Deviation from isometry was indicated by a scaling component (κ) significantly different from one in the allometric equation $FA = \gamma \text{size}^\kappa$ (Niklas 1994).
6	Use multiple regression (MR) regardless of the strength of FA–size relations.
7	Use MR only when FA–size relations are significant. *Use rule 7 if inverse size–quality relations exist and CV is large.
8	First, take residual size after removing relation between size and quality. Use FA_{rel} if FA–residual size relations are significant; otherwise use FA_u .
9	First, take residual size after removing relation between size and quality. Use MR if FA–residual size relations are significant; otherwise use FA_u . *Use rule 9 if positive size–quality relations exist and CV is large.
10	Correct for size when FA–size relations are significant; otherwise use FA_u . If FA–size relations are significant, use FA_{rel} only when FA–size relations are isometric; otherwise use MR. Deviations from isometry determined as for rule 4.
11	Correct for size when FA–size relations are significant; otherwise use FA_u . If FA–size relations are significant, use FA_{rel} only when FA–size relations are isometric; otherwise use MR. Deviations from isometry determined as for rule 5.

relations ($\alpha:\beta=0:10$), type I errors were approximately as predicted, regardless of which rule was used (figure 1a and Appendix B). Further, FA–size relations did not greatly affect power ($RP > 80\%$), and power differed only marginally between rules ($DP < 15\%$; figure 1b and Appendix B). In contrast, when size and quality related positively ($\alpha > 0$), indiscriminately using FA_{rel} (rule 2) resulted in inflated type I errors (as high as 84%; Appendix B) when underlying FA–size relations were less than isometry ($b > 0$; figure 1c). Type I errors as high as 17% and 29% occurred if FA_{rel} was used when FA–size relations did not differ significantly from isometry (rules 4 and 5, respectively). Thus, I did not consider rules 2, 4 and 5 for examining power.

Rules 1, 3, 6 and 7 yielded predicted or conservative type I error rates (figure 1c). However, power of detecting FA–quality relations was severely reduced (figure 1d). If allometric relations were not removed (rule 1), RP could be as low as 2% (Appendix B). Although there were benefits if size corrections were conducted when FA–size relations were significant (figure 1d), RP values could still be as low as 9% (rule 3) and 15% (rule 7) (Appendix B). In contrast, MR (rule 6) yielded greater power when FA–size relations were strong, but weaker power when FA–size relations were weak or absent (figure 1d and Appendix B). Thus, when size related positively with quality, correcting for allometry was important. However, rules currently used to determine whether size correction should be conducted were inefficient.

4. ALTERNATIVE RULES TO CONTROL FOR ALLOMETRY

Rules may be inefficient if underlying FA–size relations are not detected. If size relates positively to quality, FA–size relations can obscure FA–quality relations because

size and quality theoretically have opposite effects on FA (figure 1d). The reverse also could occur: FA–quality relations may obscure FA–size relations; e.g. average strength of FA–size relations generated decreased from $r=0.29$ to $r=-0.04$ (r is Pearson's correlation coefficient) as FA–quality relations increased from non-existent ($\delta=0$) to strong ($\delta=10$), even though the underlying FA–size relation was identical and isometric ($a:b$ ratio=1:0). One possible solution is to remove relations between size and quality (i.e. using residual size from a size–quality regression) before testing for FA allometry. The probability of detecting relations between FA and residual size was not affected by FA–quality relations. However, the strength of FA–residual size relations diminished as the strength of size–quality relations increased (data available upon request).

I used FA_{rel} and MR when FA–residual size relations were significant (rules 8 and 9, respectively). Type I errors were only slightly inflated (maximum of 10.3% and 8.9% for rules 8 and 9, respectively) (figure 1c and Appendix B). However, power was greatest using rules 8 and 9. The minimum RP was 34% and 43% using rule 8 and 9, respectively (compared with 9% and 15% using rule 3 and 7, respectively). The maximum DP was 48% and 42% using rules 8 and 9, respectively (compared with 30% and 28% using rules 3 and 7, respectively; Appendix B). I also considered partial regressions removing size from FA. However, this was consistently weaker than FA_{rel} or MR (although type I error rates were comparable to MR), and thus is not presented.

Next, I examined FA–size relations greater than isometry ($FA \propto \text{size}^2$). I used strong quality–size relations ($\alpha:\beta$ ratio=6:4) with no component of DN independent of size ($b=0$) and a sample size of 100. These parameters resulted in the greatest consequences of allometry in the above analysis. Rule 9 yielded considerably better power

Figure 1. (a, c) Type I errors ($\delta=0$), and (b, d) power (% significant) of rules (table 1) are illustrated as underlying FA-size relations increasing from no relation ($a:b=0:1$) to isometry ($a:b=1:0$) to $FA \propto size^2$. Relations are shown in (a, b) in the absence of size-quality relations ($\alpha:\beta=0:1$), and in (c, d) in the presence of strong positive size-quality relations ($\alpha:\beta=6:4$, average size-quality relation; $r=0.83$). Rules 1–9 are symbolized by: 1, crosses; 2, open, upright triangles; 3, open circles; 4, filled circles; 5, filled diamonds; 6, filled squares; 7, open, inverted triangles; 8, open diamonds; 9, open squares. The horizontal line represents predicted type I error rate. Type I errors were similar for all rules and were not inflated in (a), but were highly inflated for rules 2 (open, upright triangles), 4 (filled circles), and 5 (filled diamonds) in (c). Thus, power was examined only for rules 1, 3 and 6–9. Power was similar in the absence of size-quality relations (b). In contrast, when size-quality relations were strong (d), rules 3 (open circles) and 7 (open, inverted triangles) were marginally more powerful than rule 1 (crosses) when FA-size relations were less than or equal to isometry. Rule 7 was much more powerful when $FA \propto size^2$. Rule 6 (filled squares) was more powerful when FA-size relations were stronger, but less powerful when FA-size relations were weaker. Rules 8 (open diamonds) and 9 (open squares) yielded similar power for FA-size relations that were less than or equal to isometry. Rule 9 was the most powerful overall when all parameter sets were considered. Power is presented only for $\delta=1$ (other values of δ yielded similar trends). Each data point represents 1000 simulations.

than rule 8. RP ranged from 2% to 54% for rule 8, and from 39% to 74% for rule 9 (Appendix B). Both yielded predicted or conservative type I error rates.

5. INVERSE SIZE-QUALITY RELATIONS

When size related inversely to quality, rule 1 could yield greatly inflated type I errors when FA-size relations existed (figure 2a). Thus, rules 4 and 5 (using FA_u in the absence of isometry) made little sense, and were modified (see rules 10 and 11, table 1). Rules 2 and 3 were conservative if FA-size relations were less than isometric; they yielded appropriate type I errors if FA-size relations were isometric, but were inflated when $FA \propto size^2$ (figure 2a). Rules 8 and 9 also resulted in inflated type I errors (correcting for allometry when FA-residual size relations were significant). Only rules 6 and 7 yielded expected type I error rates across all parameters examined

(figure 2b). Thus, when size related inversely with quality, raw values of size were needed and residual size was not appropriate.

Use of FA_{rel} (rule 3) only failed when FA-size relations were greater than isometry. Thus, I considered rules that corrected for allometry when FA-size relations were significant, but used either FA_{rel} or MR depending on deviations from isometry (rules 10 and 11, table 1). Type I errors were improved but still inflated (maximum error rates were 18.4% and 39.2% for rules 10 and 11, respectively).

Because FA_u had inflated type I error rates when FA-size relations existed, DP was invalid. Thus, I only presented RP (FA_u had expected type I error rates in the absence of FA-size relations). RP could be reduced by more than half by using MR (figure 2c). Correcting for size when FA-size relations were significant (rule 7) yielded little difference compared with always using MR (rule 6). This was because when size related inversely

Figure 2. (a, b) Type I errors ($\delta=0$) and (c) relative power (RP) of rules (table 1) are illustrated as underlying FA-size relations increasing from no relation ($a:b=0:1$) to isometry ($a:b=1:0$) to $FA \propto size^2$. Because rule 1 had inflated type I errors, rules 4 and 5 were excluded and absolute differences in power (DP) also are not shown (see text). RP is presented only for rules 6 and 7 (other rules had greatly inflated type I errors). Horizontal line represents predicted type I error rate. Rules 1–9 are symbolized as in figure 1; rule 10, filled, upright triangles; rule 11, filled, inverted triangles. Relations were in the presence of strong inverse size–quality relations ($\alpha:\beta=-6:4$). RP was examined only for $\delta=1$ (other values of δ yielded similar trends). Each data point represents 1000 simulations.

with quality, inverse FA–quality relations indirectly inflated the strength of positive FA–size relations.

6. THE COEFFICIENT OF VARIATION OF SIZE

I examined the coefficient of variation of size ($CV=(\sigma/\bar{x}) \times 100\%$, where σ was standard deviation and

$\bar{x}$ was sample mean). I incrementally increased underlying mean size (μ in equation (4)) from 10 to 100. This resulted in a decrease in CV from 23% to 2% ($\alpha:\beta=\pm 6:4$, $a:b=1:0$, $N=100$). I examined RP for rules with predicted type I errors in the above analysis. I also examined type I error rates for the most common rules (rule 1, FA_u ; and rule 2, FA_{rel}) for inverse and positive size–quality relations, respectively.

As CV decreased, the strength of FA–size relations decreased as did the effect of allometry on power and type I error rates of FA_u (rule 1) and FA_{rel} (rule 2) (figure 3a). Thus, at low CV, size corrections using FA_{rel} may not be important. In contrast, reductions in RP were dependent upon the strength of size–quality relations rather than CV, using rule 6 or 7 (if size related inversely with quality) and using rule 6 (if size relates positive with quality). For positive size–quality relations, using rule 9 was stronger than rule 1 regardless of CV (figure 3).

7. DISCUSSION

Allometry is important because asymmetry may increase with trait size. Thus, researchers need to separate relations between FA and quality from relations between FA and size. I examined 48 studies (not including studies using trait size as a measure of quality) and found 18 studies that corrected for size using FA_{rel} in part of their study, and four using other methods (i.e. partial regressions, multiple regression, ANCOVA). Twenty studies did not assay for FA–size relations, one study by McLachlan & Cant (1995) found a relation greater than isometry ($FA \propto size^{2.5}$), and the others used significance of FA–size relations to indicate presence (or absence) of allometry. Only 20 studies tested for size–quality (or stress) relations. Eleven found that size related positively with quality (or size decreased with stress), seven found no relation, and two found inverse relations.

Allometry clearly has not been addressed adequately, given the methodology used in existing studies and given the results of this paper; e.g. if isometry exists and FA is not corrected, up to 98% of the power could be lost if positive size–quality relations exist, or type I errors could be up to 77% if inverse size–quality relations exist. Inappropriately using FA_{rel} can yield type I errors as high as 85% or may result in 98% loss of power depending on direction of size–quality relation. Researchers typically use significance of FA–size correlations to detect allometric relations. However, this may yield little benefit when inverse FA–quality and positive size–quality relations exist (as appears to be the most common scenario, see above). FA–quality and FA–size relations partly cancel one another out such that both could appear non-significant. Thus, allometry may remain undetected and uncorrected. Further, as noted by Møller (1992) and Swaddle *et al.* (1994), corrections using FA_{rel} is theoretically only appropriate if FA–size relations are isometric. Moreover, one component of FA measures is measurement error. FA_{rel} would be biased also if measurement error did not scale isometrically with size. If we could determine when isometry existed, FA_{rel} could be the most powerful index. Unfortunately, standard methods to detect deviations from isometry appear unreliable and

Figure 3. (a) Relations are shown between coefficient of variation of size (CV) and strength of FA–size relations (Pearson's r). FA–size relations were unconfounded by FA–quality relations: $\delta=0$. Relations are also shown between CV and type I error rates of FA_u (rule 1) when size–quality relations were inverse ($\alpha:\beta=-6:4$), and FA_{rel} (rule 2) when size–quality relations were positive ($\alpha:\beta=6:4$). (b, c) Relations are shown between CV and relative power (RP; for $\delta=1$) of rules for positive size–quality relations (b) and inverse size–quality relations (c). FA–size relations simulated were isometric ($a:b=1:0$). RP is presented only for rules with reasonable type I errors (see figures 1 and 2). Rules are symbolized as in figure 1. Each data point represents 1000 simulations.

using FA_{rel} can result in inflated type I error rates (rules 4, 5, 10 and 11).

The decision of which rule to use requires consideration of trade-offs between the possibility of inflated type I error rates and power. Trade-offs depend on strength and direction of size–quality relations, strength of FA–size (or residual size) relations and CV (see table 1 for

suggested rules to use under different conditions). If size does not relate to quality, corrections for size will have only marginal effect on power or type I error rates, regardless of underlying relations between FA and size. If size relates to quality, CV is important. As CV decreases, potential consequences of allometry decrease, underlying magnitudes of FA–size correlations decrease and consequences of correcting for allometry using FA_{rel} decrease. In contrast, reduction in RP using MR depends on the strength of size–quality relations and not on CV, because variation in quality is removed along with size (Palmer 1994; in addition, see Neter *et al.* (1983) for discussion on multicollinearity). Thus, for low CV, MR may sometimes be disadvantageous. When size relates inversely to quality, inverse FA–quality relations may inflate the probability of finding positive FA–size relations and size corrections may appear necessary even if no underlying FA–size relation exist. One potential solution is to use MR (rule 7) when CV is high but to use FA_{rel} (rule 3) when CV is low (note that low CV is subjective, but see figure 3). Although FA_{rel} is biased when underlying FA–size relations differ from isometry, this bias decreases as CV decreases. For high CV, MR may be necessary as the consequences of using FA_{rel} can be great (e.g. 78% type I errors when $CV=23\%$ and $FA \propto size^2$). In contrast, for positive size–quality relations, MR (rule 9) should be more powerful than rule 1 regardless of CV (but see cautions below). This is because when CV is low, FA–size relations are significant less often and MR is used less often, thus cancelling negative consequences of MR.

8. CAUTIONS AND OTHER THEORETIC CONSIDERATIONS

The conclusions of this paper necessarily are dependent upon underlying assumptions. Here, I discuss limitations of this model and problems that require further considerations. First, although I have suggested use of MR to control for allometry, its use must be approached with caution. For example, deviations from linearity could invalidate simple MR (Neter *et al.* 1983). Although I found that MR was robust to the nonlinear scenario where $FA \propto size^2$, many other possible curvilinear relations exist, which were not explored in this model. However, some curvilinear relations would not be expected owing to size scaling (FA should be positively related to size because larger individuals have greater opportunity to be asymmetric), and it would be questionable whether size corrections should be conducted where size does not causally influence FA (e.g. U-shaped FA–size curve). Nevertheless, it is possible to examine size relations and use transformations or more complex models if curvilinear relations exist (Neter *et al.* 1983). In addition, I did not examine consequences of allometry on other forms of asymmetry (antisymmetry or directional asymmetry (Palmer 1994)).

Another problem occurs when there is strong interdependence between independent variables (i.e. multicollinearity); FA–quality relations could not be interpreted except in the context of size (Neter *et al.* 1983). Whereas MR had appropriate type I error rates when FA was causally dependent on size, type I error rates could be inflated when FA and size were correlated indirectly;

e.g. if FA and size were related through some common unknown variable and if size was related to quality through another independent unknown variable, then FA would relate spuriously to quality using MR (data available upon request). Unfortunately, separation of correlation from causation may not be possible. Nevertheless, MR still offers the best option when CV is high. However, it may be better to use FA_u or FA_{rel} when CV is low.

Finally, I did not examine tests of FA differences between samples in this paper (ca. half of current studies test whether stressed samples have higher FA than unstressed samples). For FA–quality relations within samples, we can measure directly the component of quality of interest (e.g. longevity). Other unknown components of quality could relate to both size and FA, but it would be the component of interest that would determine the consequences of allometry on detection of FA relations (e.g. in the absence of longevity–size relations, underlying FA–size relations should not greatly confound FA–longevity relations). In contrast, for tests of FA differences between samples, quality would be an unmeasured quantity, and could not be removed. Hence, FA–quality relations may obscure detection of FA–size relations when positive size–quality relations exist. Solutions to this problem have yet to be determined.

This paper highlights potential consequences of allometry to FA studies, and suggests rules to correct for size. Although these rules provide advantages over current methods, they have flaws and more efficient and robust rules could be possible. Given that allometry can greatly affect power even when size corrections are conducted, I suggest researchers report CV and the strength and direction of size–quality and FA–size (residual size) relations to determine the potential effects of allometry. This is similar to arguments that measurement error

should be reported because it reduces reliability of FA (Palmer 1994).

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